Morphological variation in great ape and modern human mandibles

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ABSTRACT

Adult mandibles of 317 modern humans and 91 great apes were selected that showed no pathology. Adult mandibles of *Pan troglodytes troglodytes*, *Pongo pygmaeus pygmaeus* and *Gorilla gorilla gorilla* and from 2 modern human populations (Zulu and Europeans from Spitalfields) were reliably sexed. Thirteen measurements were defined and included mandibular height, length and breadth in representative positions. Univariate statistical techniques and multivariate (principal component analysis and discriminant analysis) statistical techniques were used to investigate interspecific variability and sexual dimorphism in human and great ape mandibles, and intraspecific variability among the modern human mandibles. Analysis of interspecific differences revealed some pairs of variables with a tight linear relationship and others where *Homo* and the great apes pulled apart from one another due to shape differences. *Homo* and *Pan* are least sexually dimorphic in the mandible, *Pan* less so than *Homo sapiens*, but both the magnitude of sexual dimorphism and the distribution of sexually dimorphic measurements varied both among and between modern humans and great apes. Intraspecific variation among the 10 populations of modern humans was less than that generally reported in studies of crania (74.3% of mandibles were correctly classified into 1 of 10 populations using discriminant functions based on 13 variables as compared with 93% of crania from 17 populations based on 70 variables in one extensive study of crania). A subrecent European population (Poundbury) emerged as more different from a recent European population (Spitalfields) than other more diverse modern populations were from each other, suggesting considerable morphological plasticity in the mandible through time. This study forms a sound basis on which to explore mandibular variation in Neanderthals, early *Homo sapiens* and other more ancient fossil hominids.

Key words: Hominoids; mandible; sexual dimorphism.

INTRODUCTION

In recent years, a number of important fossil mandibles attributed to both Neanderthals and early *Homo sapiens* have been recovered. At the same time debate about human evolution has come to focus more sharply on the origins of modern *Homo sapiens*. Potentially, fossil mandibles such as those, for example, from Heidelberg in Germany, Klasies River Mouth in South Africa, and those from Tabun, Kebara, and Qafzeh in Israel, which differ considerably in their size and morphology, may help shed light on this key issue. However, it is not clear to what extent this variation in size and morphology simply mirrors that present in modern human mandibles. Neither is it clear how certain fundamental mandibular dimensions such as height, breadth and length, relate to mandibular size and to each other and to what extent apparently contrasting mandibular morphologies may simply be a consequence of body size and sexual dimorphism. Despite the fact the mandible is better represented in the the hominid and hominoid fossil record than most other bones there are still many more comparative studies of the cranium than there are of the mandible.

To explore these issues we have undertaken a

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comparative study of a large and diverse sample of modern human mandibles. We compared these human samples with samples of modern great ape mandibles to provide a broader comparative framework that we judge will be useful in interpreting a sample of fossil hominid mandibles. In this paper we document and compare the extent of inter and intraspecific variation in mandibular shape and size, and examine the magnitude and distribution of sexual dimorphism in reliably sexed samples of gorillas, chimpanzees, orang–utans and 2 modern human populations. In a second paper we will examine morphological variation in fossil hominid mandibles with respect to the sample described here.

The literature documenting variation in human mandibular morphology is extensive and includes comparative studies on hominoid fossils, both qualitative and quantitative comparative studies on the nature of sexual dimorphism in primates as well as studies that are primarily aimed at relating mandibular morphology to biomechanics and masticatory function. It is not our intention here, nor would it be possible, to review all the literature that has included work on mandibular morphology. However, in no previous study has there been a comprehensive review of the literature relating specifically to descriptive and morphometric studies of human and great ape mandibles and so for this reason we focus our review specifically on these comparative studies.

Morphometric studies of the mandible

The earliest contributions to mandibular morphometrics were aimed not simply at documenting population and sex differences in mandibular morphology, but rather at using mandibular measurements as a vehicle to explore and develop new statistical methods and techniques (Martin 1936; Morant et al. 1936). Few of these early studies were able to use mandibles that were reliably sexed and even fewer extended comparisons of human mandibular morphology to nonhuman primates. In an early attempt to document population differences in mandibular morphology, Harrower (1928) examined a large sample of mandibles from 4 Asian groups and concluded that, despite profound differences in cranial morphology in these groups, the mandibles showed a 'much more constant structure' with near identical mean values of the measurements made in each group. Cleaver (1937) examined mandibular variation in 17 male and 9 female series and emphasised that, despite this large number, the mandible was less useful for describing population differences than the cranium.

Mandibles tended, Cleaver concluded, to be more variable relative to size than crania, exactly the opposite conclusion to Harrower's (1928) more limited study.

Hrdlička (1940b) regarded the mandible as 'the neglected stepchild of anthropometry' and considered the samples studied thus far to be 'small'. In 3 contributions Hrdlička (1940a,b,c) documented mandibular (and maxillary) hyperostoses, measured angles of the mandible and provided additional data on linear measurements and ratios of 4541 male and female mandibles from 24 different human populations. Hrdlička concluded that mandibular variation in linear measurements could safely be accepted as mainly ontogenetic and of 'functional causation connected with masticatory function', and that it bears little relation to stature or head shape and shows 'no marks of phylogenetic or evolutionary phenomena' (Hrdlička, 1940b,c). Hrdlička's exhaustive studies may have had the effect of discouraging any further attempts to use the mandible rather than the cranium in forensic studies or in tracing the origins of human populations. A few subsequent studies have provided detailed metrical and nonmetrical data describing variation in mandibular morphology in particular human populations (Lee & Choi, 1961; Aitchison 1964, 1965a; Chang & Lee, 1990; Murphy, 1957), but it is notable that there have been no further attempts to document geographical variation in human mandibular morphology across a wider range of human populations using appropriate statistical methods.

Most descriptions of great ape mandibles have been made in a comparative context with the primary aim of describing fossil hominid remains and few exist that describe differences between them. Aitchison (1963a, 1965b) attempted to describe differences between great ape mandibles qualitatively and noted a relationship between the height of the ascending ramus and the level of the occlusal plane in great apes. In *Pongo* the occlusal plane lies at a level approximately midway between the highest and lowest points of the ascending ramus whereas in *Pan*, which has the least tall ascending ramus of the 3 great apes, the level of the occlusal plane divides it into a large lower and a small upper portion. In *Gorilla*, which has the tallest ascending ramus, Aitchison noticed the occlusal plane divides it into a small lower and large upper portion. Great ape and human mandibles also grow in different ways. In juvenile chimpanzees the mandibular angle is low but during growth it increases as the body and ramus increase in length. This is the reverse of what happens in humans who begin with a high angle which

then reduces as the ascending ramus becomes more upright. In addition, Aitchison drew attention to the especially low position of the mental foramen and myohyloid line in *Pan* and described other details of the dentition, dental arch shape and mandibular condyles in great apes. Kinzey (1970) examined the size and shape of the mandibular dental arch in a large sample of living and fossil primates and quantified the differences between *Pan*, *Gorilla*, *Pongo* and *Homo sapiens* graphically.

Temporal variation in mandibular morphology

Moore et al. (1968) recorded a reduction in mandibular size in British populations between the Neolithic and 19th century, which was particularly pronounced for dimensions of the mandibular ramus. Lavelle (1972) examined variation in human mandibular morphology in 3 British samples, and demonstrated a decrease in mandibular size between the Romano–British period and 19th century. However, he was unable to establish exactly which components of the mandible had reduced in size and therefore could not determine whether the body of the mandible remained unchanged, despite the fact that the teeth, which lie within the mandibular body, have not reduced in size. Kaifu (1997) examined changes in mandibular morphology in Japanese populations from the Jomon to modern periods, and attributed an increase in symphyseal height in protohistoric and medieval groups to the effects of a limited genetic contribution from Yayoi immigrants and more general size reduction to environmental factors, specifically a reduction in chewing stresses.

Studies of mandibular sexual dimorphism

One of the first informative comparative studies of modern human and great ape mandibles was that of Weidenreich (1936) in his monograph on the '*Sinanthropus*' mandibles from Zhoukoudian. Weidenreich used data from Schreiner (1931/35) for male and female Lapps and from Shima (1933) for male and female Koreans, Chinese and Japanese. On the basis of these data for modern humans, Weidenreich concluded that modern human female mandible size averaged 92.4% of male size. The size of female '*Sinanthropus*' mandibles on the other hand appeared to be only 85.9% of that of males, indicating higher sexual dimorphism in this species. Weidenreich presented similar data on average mandibular sexual dimorphism in the great apes: 78% in orang utans, 80% in gorillas and 87% in chimpanzees (but on what he admitted was a poor sample of the latter).

Morant et al. (1936) made angular and linear measurements on 2 series of ancient Egyptian mandibles. Their aim was to explore the usefulness of new methods to calculate coefficients of variation and correlations rather than to say anything in particular about population or sex differences. However, these authors did single out height of the ramus as especially variable between the sexes, although their sample was sexed using anatomical criteria. In another study on the same Egyptian mandible sample, Martin (1936) paid further attention to the mathematical methods of sexing mandibles from angular and linear measurements. Martin concluded that the mandible was better for mathematical sex determination than the cranium and that measurements of the overall height of the mandible were best used for this purpose. Hrdlička (1940b,c) evaluated sexual differences in gonial angle and several mandibular dimensions and found consistent differences between males and females from a diverse range of human groups. Sexual differences were low in the breadth and length of the mandibular body, higher in symphyseal height and highest in the height of the ramus. Regarding the gonial angle, Hrdlička (1940b) concluded that it is of limited value for sex determination and that 'all that can be said is that a gonial angle of less than 118 degrees points towards a male, above 128 degrees towards a female, but there are numerous exceptions'. Aitchison (1963b) made claims for a 'consistent difference' between males and females in the depth of the mandibular (sigmoid) notch and the distance between the coronoid and condylar processes. However these were qualitative observations and have never been tested metrically on any large human samples of known sex.

The early findings of Morant et al. (1936), Martin (1936) and Hrdlička (1940b,c) have subsequently been confirmed in more thorough studies by De Villiers (1968a,b) and Hunter & Garn (1972) using reliably sexed samples. Measurements of the height of the mandibular ramus tend to show higher sexual dimorphism than measurements of body height and breadth, and differences between the sexes are generally more marked in the mandibular ramus than in the mandibular body (De Villiers, 1968a,b). Giles (1964) calculated discriminant functions to classify mandibles from the Terry Collection as male or female with 85% accuracy and identified the heights of the mandibular symphysis, ramus and body, together with mandibular body length and bigonial diameter as particularly useful measurements for this purpose. Hanihara (1959) used discriminant functions to classify Japanese crania as male or female. He obtained a similar level of accuracy to Giles (1964)

using only 4 measurements of the mandible but, surprisingly, obtained a higher level of accuracy using a combination of measurements from the calvarium and mandible.

Wood (1976) included mandibular dimensions in his analysis of sexual dimorphism in the primate skeleton, and concluded that sexual dimorphism in shape was predominantly the result of allometric relationships (i.e. differential size). Wood et al. (1991) have carried out the most comprehensive comparative metrical study of hominoid mandibles using a large sample of individuals of known sex. Their data demonstrate that human mandibles (South Africans from the Nguni and Sotho tribes) and those of chimpanzees are less dimorphic than those of gorillas and orang-utans. Humans and chimpanzees followed one pattern of dimorphism, and gorillas and orang utans another in this study. When the data were examined in multivariate space using canonical variates however, humans emerged as distinct from the other 3 species.

In a recent study of sexual dimorphism in the human mandible, Loth & Henneberg (1996) have claimed an astonishing 94.2% accuracy for sexing the mandibles of a combined African and American sample (including whites, blacks and native Americans) using a single character. Their study suggested that the degree of flexure of the posterior border of the ramus at the level of the occlusal plane of the teeth is as reliable for sex determination as the pelvis. More recently, Muller (1998) tested procedures for determining sex from a single mandibular character and found that gonial flaring provides a more accurate indicator of sex (76%) than either chin shape or ramal flexure. Donnelly et al. (1998) undertook a blind test of mandibular ramus flexure as a predictor of sex, and reported that the association between sex and ramus flexure was weak and that the trait could not be consistently identified.

Aims of this study

Overall, this literature presents a rather confused picture of morphological variation in the lower jaw and highlights the need for a new and broader study on the mandible of extant hominoids. The aims of this study are (1) to provide a broad data base of human and great ape mandibular measurements that includes a diverse range of human populations, and to provide basic sample statistics for each on which future studies of fossil hominid mandibles can be based; (2) to explore metrical data for 2 human populations of known sex (Spitalfields and Zulus) that have not been studied previously in a wider comparative context and to compare their patterns of dimorphism with each other and with those of the great apes; and (3) to test the hypothesis that the mandible is less useful than the cranium in providing information about regional variation in modern humans using newer and more appropriate statistical methods than previous studies.

MATERIALS

Mandibles used for this study were selected on the basis of the criteria outlined by Wood et al. (1991). Only mandibles from individuals with the upper and lower third molars in occlusion were measured and mandibles which were obviously distorted by pathological conditions including antemortem tooth loss were excluded from this study. The samples used for the analysis of sexual dimorphism were sexed on the basis of nonosteological criteria (Jenkins, 1990). The ape specimens from the Powell-Cotton Museum were sexed from field records and associated soft tissue remains. The specimens at the Natural History Museum were sexed on the basis of field records, associated soft tissue remains and dental morphometrics. The Zulu sample was sexed on the basis of nonosteological dissecting room records. The Spitalfields sample was sexed on the basis of associated coffin plates and supporting documentary evidence (Molleson & Cox, 1993). The following 10 modern human and 3 great ape samples were included in the study. (1) African mandibles from Gabon, West Africa (33 individuals) housed at the Natural History Museum, London; Zulus, South Africa (14 males and 16 females) housed in the Dart Collection in The Department of Anatomy, The University of Witwatersrand; Bushman, South Africa (18 individuals) housed in the Department of Anatomy, The University of Cape Town and in the Dart Collection; Nubians, Middle Nile city of Kerma, North Africa (40 individuals) housed in the Duckworth Collection, Department of Biological Anthropology, University of Cambridge. (2) European mandibles from Spitalfields, London, UK (15 males, 15 females) and from Poundbury, Dorset, UK (50 individuals) both housed at the Natural History Museum. The Spitalfields sample comprises urban living individuals of British and French ancestry who were buried in Christ Church, Spitalfields, between 1729 and 1852 (Molleson & Cox, 1993). The Poundbury sample comprises rural living individuals from the Romano–British period, who lived approximately 1400 years earlier than the Spitalfields individuals (Farwell & Molleson, 1993). (3) Asian/Arctic mandibles from
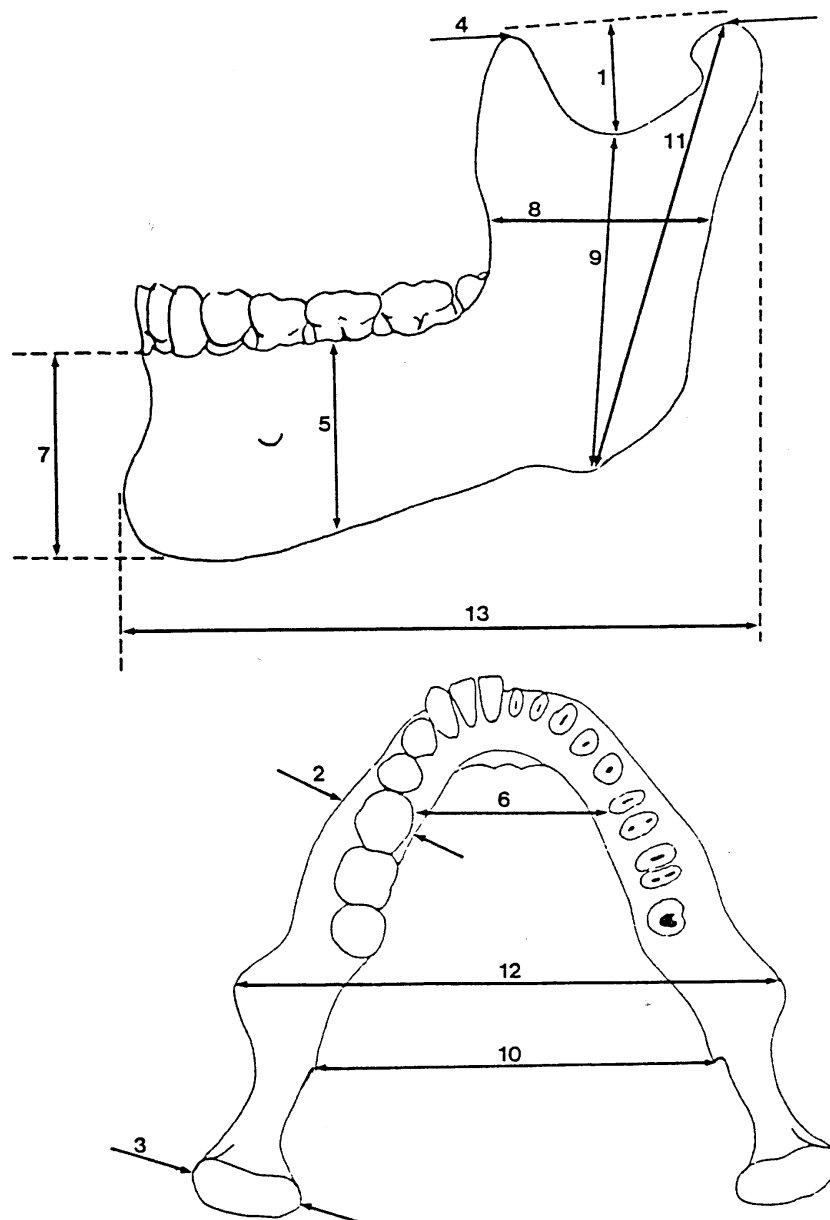
Fig. 1. Measurements.

Chinese (18 individuals) housed in the Dart Collection, and Greenland Eskimos (27 individuals) housed at the Natural History Museum. (4) Polynesian mandibles from Chatham Islanders (33 individuals) housed at the Natural History Museum. (5) Australian mandibles from Australian Aborigines (38 individuals) housed in the Duckworth Collection. (6) Mandibles from *Pongo pygmaeus pygmaeus* from Borneo (14 males, 19 females) housed at the Natural History Museum. (7) Mandibles from *Gorilla gorilla gorilla* (13 males, 17 females) housed at the Natural History Museum and the Powell Cotton Museum, Birchington, Kent. (8) Mandibles from *Pan troglodytes troglodytes* from Cameroon (14 males, 14 females) housed at the Natural History Museum and the Powell Cotton Museum.

METHODS

Morphometric methods

With the exception of mandibular length, measurements were taken with sliding callipers to the nearest 0.1 mm. Mandibular length was measured to the nearest 1 mm using an osteometric board. Measurements 1–5, 8, 9 and 11 were taken on the left side, except when the left side was damaged. Repeated measurements by 3 observers suggest that interobserver error varies between 0.3% and 2.8% for the 13 measurements. Height measurements were the most error prone. Occasionally one or more measurements could not be made on an individual and these cases are excluded from the analyses as necessary. The following linear measurements, illustrated in Figure 1,

Table 1. *Sample sizes, means, standard deviations, and minimum and maximum values for each of the 13 mandibular dimensions in 10 modern human population samples and three great ape samples*

	n	Mean	S.D.	Minimum	Maximum
Australian					
Notch depth	38	11.5	2.2	7.5	16.2
Body thickness	38	13.9	1.4	11.3	16.2
Condyle width	38	20.3	1.8	15.8	23.8
Coronoid-condyle	25	34.5	2.8	29	40.2
Body height	38	27.5	2.4	22.7	33.0
Mandibular breadth	38	35.6	3.5	27.7	43.7
Symphysis height	38	30.3	2.3	25.6	34.4
Ramus width	38	33.8	3.1	25.8	42.0
Notch height	38	47.3	4.4	40.7	57.2
Bilingual breadth	25	79.0	5.3	71.2	89.2
Ramus height	38	63.5	4.3	56.8	71.3
Bicoronoid breadth	25	95.2	5.5	84.0	106.0
Mandibular length	38	104.6	5.5	97.0	116.0
Bushman					
Notch depth	18	11.9	2.5	9.0	18.2
Body thickness	18	12.7	1.2	10.5	15.0
Condyle width	12	18.3	2.2	14.0	22.5
Coronoid-condyle	14	33.1	3.1	26.0	37.0
Body height	17	27.1	3.4	16.7	33.0
Mandibular breadth	18	32.7	3.0	27.4	39.0
Symphysis height	17	31.9	4.9	20.0	45.0
Ramus width	18	34.9	3.3	28.0	41.0
Notch height	18	39.8	5.0	31.0	49.0
Bilingual breadth	18	73.0	4.5	65.0	82.0
Ramus height	18	55.8	6.1	45.0	69.0
Bicoronoid breadth	14	89.8	5.4	81.0	105.0
Mandibular length	18	98.3	7.5	82.0	115.0
Chinese					
Notch depth	18	13.6	1.9	11.0	17.0
Body thickness	18	14.3	1.4	12.0	17.0
Condyle width	17	19.4	2.4	14.0	24.0
Coronoid-condyle	18	34.9	2.5	30.0	41.0
Body height	18	31.1	2.3	27.0	36.0
Mandibular breadth	18	34.9	2.0	32.0	39.0
Symphysis height	18	34.2	2.3	31.0	39.0
Ramus width	18	33.8	2.4	31.0	39.0
Notch height	18	50.9	3.8	46.0	60.0
Bilingual breadth	18	77.2	3.2	72.0	83.0
Ramus height	18	71.1	4.6	64.0	81.0
Bicoronoid breadth	18	93.8	4.3	86.0	101.0
Mandibular length	18	103.3	5.4	92.0	114.0
Eskimo					
Notch depth	27	12.3	1.5	9.0	15.6
Body thickness	27	14.4	1.8	10.6	18.8
Condyle width	27	20.7	1.6	17.5	24.4
Coronoid-condyle	26	40.3	3.3	35.0	48.5
Body height	27	31.0	3.4	24.5	39.8
Mandibular breadth	27	36.2	2.8	29.0	43.1
Symphysis height	27	35.0	2.6	30.8	41.5
Ramus width	27	41.0	3.3	35.1	49.9
Notch height	27	45.9	4.6	37.3	53.8
Ramus height	27	64.2	5.6	53.5	77.1
Bilingual breadth	26	85.7	4.3	75.0	94.0
Bicoronoid breadth	26	97.3	5.8	89.0	107.0
Mandibular length	27	108.8	5.0	100.0	118.0
Gabon					
Notch depth	33	12.5	1.7	9.3	15.7
Body thickness	33	13.7	1.3	11.2	17.3
Condyle width	33	19.4	1.7	16.6	22.9
Coronoid-condyle	33	31.7	3.4	25.2	42.0

Table 1 (*cont.*)

	n	Mean	S.D.	Minimum	Maximum
Body height	32	26.2	3.9	18.5	36.3
Mandibular breadth	33	37.4	2.1	34.6	41.6
Symphysis height	33	29.9	4.6	17.7	38.5
Ramus width	33	33.5	2.6	28.1	38.5
Notch height	33	44.7	4.9	36.1	55.0
Bilingual breadth	33	74.5	3.7	68.0	82.0
Ramus height	33	60.1	4.8	51.2	70.0
Bicoronoid breadth	33	93.0	5.3	82.0	103.0
Mandibular length	33	100.5	7.0	83.0	114.0
Nubian					
Notch depth	40	12.6	1.5	9.5	16.6
Body thickness	40	12.5	1.3	10.0	15.3
Condyle width	40	19.9	1.8	15.0	23.0
Coronoid-condyle	40	34.4	2.8	26.7	40.0
Body height	40	26.6	3.1	18.5	32.4
Mandibular breadth	40	36.5	2.9	27.9	42.4
Symphysis height	40	29.5	3.5	20.7	34.8
Ramus width	40	33.5	3.3	22.3	38.8
Notch height	40	47.6	6.6	37.5	63.2
Bilingual breadth	40	74.2	5.1	65	83.2
Ramus height	40	61.2	7.0	47.4	79.3
Bicoronoid breadth	40	92.2	5.6	83.0	102.0
Mandibular length	40	102.7	5.1	93.0	118.0
Polynesian					
Notch depth	33	14.2	2.7	9.4	22.2
Body thickness	33	14.0	1.3	11.7	16.4
Condyle width	33	21.6	2.5	16.2	26.6
Coronoid-condyle	33	28.8	3.8	21.2	37.7
Body height	33	31.6	3.9	25.8	42.2
Mandibular breadth	33	36.2	2.2	30.6	41.4
Symphysis height	33	32.0	3.7	26.2	41.9
Ramus width	33	36.5	3.0	32.1	43.6
Notch height	33	46.1	7.7	32.0	63.9
Bilingual breadth	33	79.7	5.3	67.3	89.2
Ramus height	33	68.6	7.5	57.2	85.6
Bicoronoid breadth	33	94.2	7.5	81.3	107.0
Mandibular length	33	106.4	6.6	94.0	122.0
Poundbury					
Notch depth	50	12.9	1.7	9.6	18.4
Body thickness	50	13.3	1.7	10.2	17.0
Condyle width	50	20.1	2.7	14.3	26.3
Coronoid-condyle	45	32.5	3.2	27.4	38.2
Body height	50	27.8	2.9	22.5	36.3
Mandibular breadth	50	40.2	3.4	28.1	48.6
Symphysis height	50	29.9	3.1	24.5	38.5
Ramus width	50	31.5	3.0	25.4	38.3
Notch height	50	49.8	6.3	36.8	65.3
Bilingual breadth	47	82.5	4.7	71.4	93.4
Ramus height	50	65.2	6.5	51.1	78.3
Bicoronoid breadth	43	101.4	7.1	90.0	119.0
Mandibular length	47	101.6	6.2	91.0	113.0
Spitalfields					
Notch depth	30	12.3	1.7	8.9	16.3
Body thickness	30	12.4	1.5	9.7	16.3
Condyle width	30	19.4	2.2	14.7	24.7
Coronoid-condyle	30	25.9	3.4	21.0	32.0
Body height	30	28.4	2.8	23.6	34.4
Mandibular breadth	30	37.0	2.7	32.0	42.5
Symphysis height	30	31.7	3.5	25.8	39.0
Ramus width	30	29.0	3.4	22.8	35.3
Notch height	30	43.6	5.0	35.5	52.2
Bilingual breadth	30	75.1	6.0	63.4	88.8

Table 1 (*cont.*)

	n	Mean	S.D.	Minimum	Maximum
Ramus height	30	66.7	5.4	57.2	77.0
Bicoronoid breadth	30	90.6	5.3	79.6	102.0
Mandibular length	30	100.0	7.2	87.0	115.0
Zulu					
Notch depth	30	12.2	1.8	9.3	17.4
Body thickness	30	12.9	1.4	10.5	15.6
Condyle width	30	19.4	2.2	15.0	25.0
Coronoid-condyle	30	33.6	3.4	24.0	39.0
Body height	30	30.3	3.6	21.5	37.3
Mandibular breadth	30	34.3	1.9	31.0	39.0
Symphysis height	30	34.1	3.1	27.0	40.0
Ramus width	30	35.1	3.4	29.0	44.0
Notch height	30	43.8	5.7	32.0	55.0
Bilingual breadth	30	74.1	4.3	65.0	85.0
Ramus height	30	61.4	6.8	43.0	76.0
Bicoronoid breadth	30	92.5	3.8	85.0	101.0
Mandibular length	30	104.8	6.5	92.0	117.0
Gorilla					
Notch depth	30	18.4	4.2	12.8	27.4
Body thickness	30	18.1	1.5	15.5	22.0
Condyle width	30	32.8	5.1	24.3	50.0
Coronoid-condyle	29	36.4	5.0	29.2	50.5
Body height	30	38.2	5.2	28.8	49.9
Mandibular breadth	30	32.1	2.4	27.4	36.0
Symphysis height	30	46.4	7.7	32.7	62.0
Ramus width	30	60.6	10.4	49.3	87.8
Notch height	30	84.3	11.7	68.3	117.5
Bilingual breadth	30	85.9	9.9	72.7	112.0
Ramus height	30	109.6	12.9	90.9	148.6
Bicoronoid breadth	30	111.2	11.1	90.3	135.0
Mandibular length	30	158.9	19.2	130.0	194.0
Pan					
Notch depth	28	11.2	1.4	8.6	14.8
Body thickness	28	13.6	1.2	11.4	16.2
Condyle width	28	22.2	1.5	19.5	25.6
Coronoid-condyle	28	34.3	4.2	25.4	43.0
Body height	28	28.3	2.5	22.8	33.8
Mandibular breadth	28	35.1	2.2	31.7	41.2
Symphysis height	28	32.1	4.0	24.8	42.0
Ramus width	28	44.0	3.9	33.6	50.8
Notch height	28	52.7	4.5	43.0	63.0
Bilingual breadth	28	71.5	4.6	63.0	80.2
Ramus height	28	69.6	5.2	57.9	83.0
Bicoronoid breadth	28	88.2	4.5	77.9	96.0
Mandibular length	28	126.0	7.1	110.0	139.0
Pongo					
Notch depth	33	13.5	2.8	9.5	22.4
Body thickness	33	15.7	1.9	13.0	22.4
Condyle width	33	27.6	4.6	21.3	38.4
Coronoid-condyle	32	40.7	5.0	32.0	52.2
Body height	33	37.9	5.2	29.0	53.8
Mandibular breadth	33	34.5	3.1	30.4	44.3
Symphysis height	33	45.8	6.8	36.1	64.5
Ramus width	33	50.8	7.7	42.4	67.3
Notch height	33	73.3	10.3	59.9	100.0
Bilingual breadth	33	76.9	7.0	65.5	91.7
Ramus height	33	95.4	12.9	80.1	123.0
Bicoronoid breadth	33	93.9	7.8	82.4	110.0
Mandibular length	33	140.1	15.5	121.0	173.0

Measurements are in mm.

were made: (1) The maximum depth of the mandibular notch from a line joining the most superior points on the mandibular condyle and the coronoid process to the lowest point of the mandibular notch (NOTD). (2) The minimum thickness of the body of the mandible measured across the 1st permanent molar tooth with the jaws of the calipers orthogonal to the occlusal plane (BODTH). (3) The maximum mediolateral width of the mandibular condyle (CONW). (4) The distance from the most superior point on the mandibular condyle to the most superior point on the coronoid process (CNCR). (5) The height of the body of the mandible from the lowest point on the crest of the buccal alveolar bone opposite the mesiobuccal root of the 1st permanent molar to the lower border of the mandible with the jaws of the calipers held parallel to the occlusal plane (BODH). (6) The bimandibular breadth between the left and right bodies of the mandible from the lowest point on the crests of the alveolar bone opposite the mesio-lingual root of the 1st permanent molar tooth (BIM1). (7) The perpendicular height of the mandibular symphysis from the alveolar crest between the 2 permanent central incisors and the lowest point of the lower border of the mandibular symphysis in the midline with the mandible placed on a level surface (SYMHT). (8) The minimum anteroposterior width of the ramus of the mandible. (RAMAP). (9) The height of the ramus of the mandible from the lowest point of the mandibular notch to the tubercle or most protruding part of the inferior border of the ramus in the mid position of the ramus (tubercle defined after Hrdlička, 1940c) (NTHT). (10) The minimum distance between the base of the right and left lingula (BILING). (11) The height of the ramus of the mandible from the most superior point on the mandibular condyle to the tubercle, or most protruding portion of the inferior border of the ramus (after Hrdlička, 1940c) (CONHT). (12) The maximum breadth of the mandible measured between the most superior points of the right and left coronoid processes (BICOR). (13) The minimum anteroposterior length of the mandible measured between a line perpendicular to the most posterior points on the mandibular condyles to a line perpendicular to the most anterior point of the mandibular symphysis and measured with an osteometric board (MANDL).

These measurements were chosen to provide a balance of height, width and breadth measures and of measurements of the mandibular ramus and body. Specific measurements were selected to explore points raised in the literature more thoroughly (e.g. notch depth, coronoid to condyle distance; see Aitchison

1963*a*,*b*, 1964, 1965*a*,*b*). All measurements could be defined unambiguously on fossil taxa. A decision was made not to make a detailed study of variation in the mandibular angle, nor of the chin and lingual symphyseal morphology. This was done in order to limit the number of measurements taken.

Statistical methods

Basic statistical parameters of each mandibular dimension in each population or species are listed in Table 1. These data are used to analyse 3 different aspects of morphological variation in the mandible. (1) interspecific variation in mandibular morphology; (2) variation in the expression of mandibular sexual dimorphism; and (3) regional and population variation within modern humans. Each of these aspects is examined using univariate and multivariate methods. All analyses were computed using raw data. Principal components analyses were based on correlation matrices. For each analysis, mandible distribution patterns were examined on each principal component with an eigenvalue greater than one. The analyses were carried out using SPSS Release 6.

RESULTS

Interspecific variation

Figure 2 shows a plot of mean size in 13 mandibular variables for *Homo sapiens*, *Pan*, *Pongo* and *Gorilla*. *Gorilla* and *Pongo* are generally larger than *Pan* and *Homo sapiens*, particularly in those dimensions which reflect height of the mandible. *Homo sapiens* displays the lowest mean values for mandibular length, the
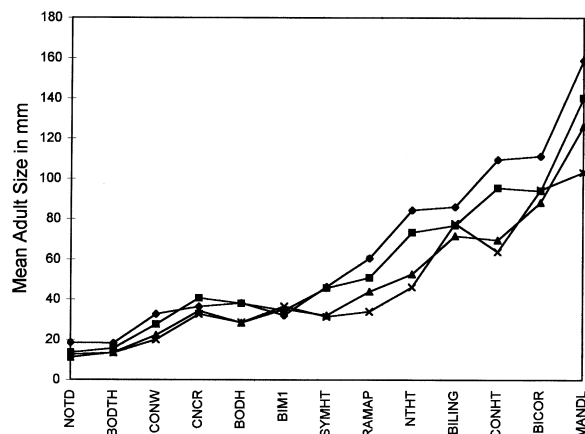

Fig. 2. Plots of mean adult size for 13 mandibular dimensions in 4 hominoid species. ◆ Gorilla; ■ Pongo; ▲ Pan; × Homo.

Table 2. *Significance of size differences in 13 mandibular dimensions between Homo sapiens, Pan, Gorilla and Pongo*

	Homo-Pan	Homo-Gorilla	Homo-Pongo	Pan-Gorilla	Pan-Pongo	Gorilla -Pongo
Notch depth	**	**	*	**	**	**
Body thickness	ns	**	**	**	**	**
Condyle width	**	**	**	**	**	**
Coronoid-condyle	ns	**	**	ns	**	**
Body height	ns	**	**	**	**	ns
Mandibular breadth	**	**	**	**	ns	**
Symphysis height	ns	**	**	**	**	ns
Ramus width	**	**	**	**	**	**
Notch height	**	**	**	**	**	**
Bilingual breadth	**	**	ns	**	**	**
Ramus height	**	**	**	**	**	**
Bicoronoid breadth	**	**	ns	**	**	**
Mandibular length	**	**	**	**	**	**

ns, nonsignificant; * significant ($P < 0.05$); ** highly significant ($P < 0.01$).

maximum heights of the mandibular ramus and notch, and the width of the ramus, and has the highest value for the breadth of mandible measured across the floor of the mouth. Student's t test was used to test for significant differences in mean values of each variable for each pair of species, using an assumption of equal or unequal variance as appropriate (Table 2). Nearly all differences between species means are significant ($P < 0.05$). Sample means are not significantly different in 4 variables in *Pan* and *Homo sapiens* (mandibular body height and thickness, symphyseal height and coronoid-condyle distance), compared with 2 variables in *Homo sapiens* and *Pongo* (bicoronoid and bilingular breadth) and *Gorilla* and *Pongo* (mandibular body and symphyseal height) and 1 variable in *Pan* and *Pongo* (mandibular breadth at M1), and *Pan* and *Gorilla* (coronoid-condyle distance). However, the size ranges of all 4 species overlap in all of the dimensions apart from mandible length, for which the size ranges of *Homo sapiens* and *Gorilla* are discrete, and the heights of the mandibular notch and ramus for which the size ranges of *Homo sapiens* and *Pan* are discrete from that of *Gorilla*.

In a series of bivariate plots, *Homo sapiens* is most clearly separated from the great apes in measurements of mandibular width against mandibular length (Fig. 3a), and by anteroposterior ramus width plotted against the distance between the coronoid process and mandibular condyle (Fig. 3b). The latter plot reflects the fact that *Homo sapiens* has a narrower ramus (anteroposteriorly) than the other species. Overall, *Homo sapiens* has a shorter and therefore relatively wider mandible than the great apes. *Pan* shows intermediate values between those of *Homo sapiens* and those of *Gorilla* and *Pongo* in ratios which measure mandibular width against height (Fig. 3c).

This reflects the fact that *Homo sapiens* and *Pan* have lower mandibular rami and bodies than *Gorilla* and *Pongo*. Several pairs of variables exhibit a tight linear relationship, although we have not examined the similarity of the slopes of each of the 4 species individually in a statistical sense. This is shown most clearly between some pairs of variables which measure either height or length of the mandible (Fig. 3d) and to a lesser extent between pairs measurements of height plotted against length. It is also true of the relationship between the width of the mandibular condyle and measurements of the length of the mandible or the height of the ramus (Fig. 3e).

Relative size of the 13 mandibular dimensions in the 4 species was compared by examining bivariate plots of the size of each variable against mandibular size in each specimen.

Mandibular size was calculated for each individual as the geometric mean (size) of the 13 mandibular dimensions. The heights of the mandibular ramus and notch and the width of the mandibular condyle exhibit a tight linear relationship with mandibular size across the 4 species (Fig. 4a). Relative to *Gorilla* and *Pongo*, *Pan* has high values for mandibular length and the minimum breadth of the ramus, and *Homo sapiens* has low values (Fig. 4b). The distributions of *Homo sapiens* and *Pan* for mandibular length plotted against mandibular size are almost entirely discrete. Relative to mandibular size, *Homo sapiens* has the highest values for bicoronoid breadth (Fig. 4c) and the same is true for bilingular breadth and the breadth of the mandible measured at M1.

Principal components analysis was used to investigate which factors, if any, discriminate between the 4 species and which variables had the highest variable loadings for those factors. On factor 1, which
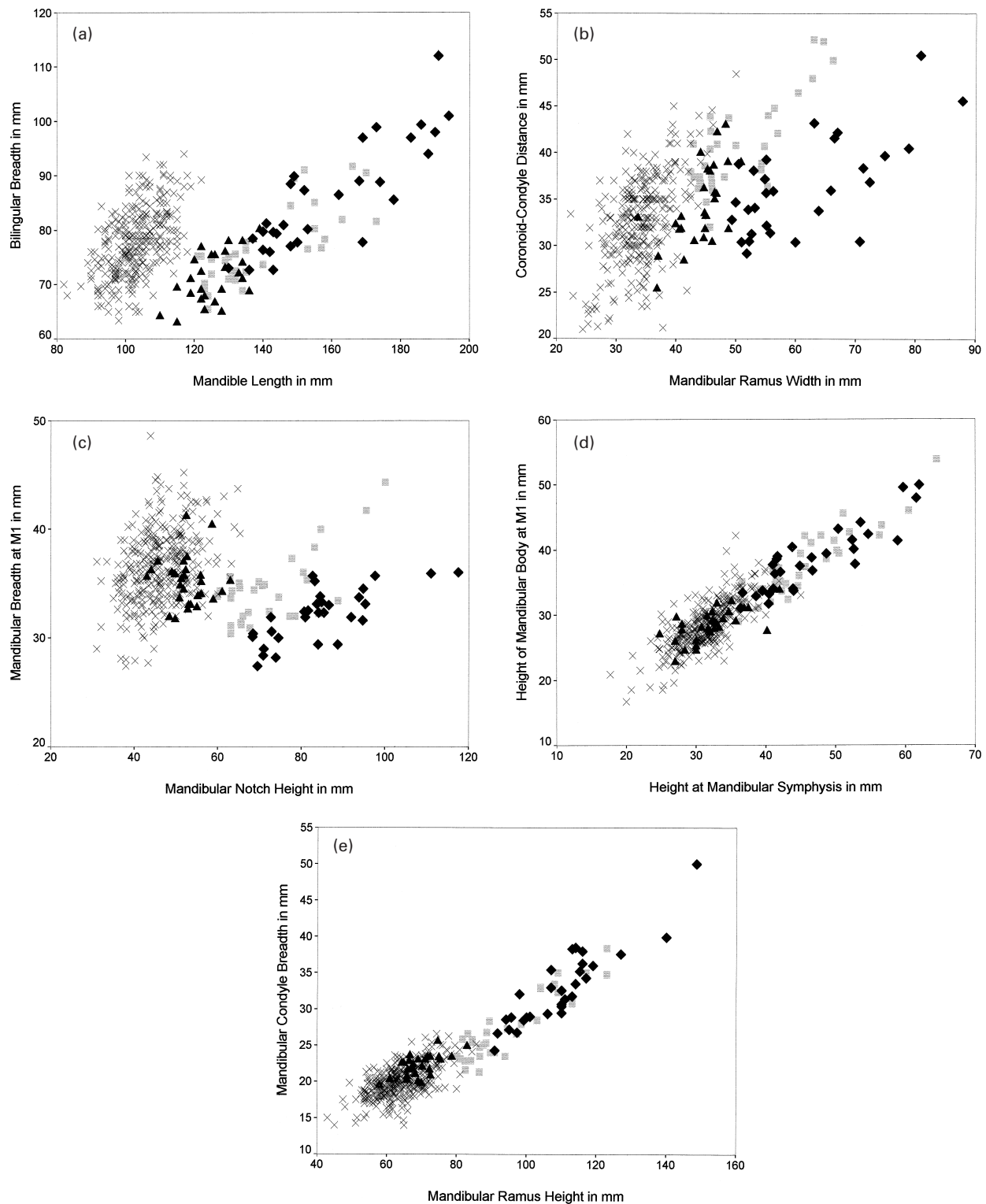
Fig. 3. Bivariate plots of mandibular dimensions in the 4 species: (*a*) bilingular breadth (BILING) plotted against mandibular length (MANDL); (*b*) condylar-coronoid distance (CNCR) plotted against mandibular ramus width (RAMAP); (*c*) mandibular breadth at M1 (BIM1) plotted against mandibular notch height (NTHT); (*d*) height of the mandibular body at M1 (BODH) plotted against height at the mandibular symphysis (SYMHT); (*e*) mandibular condylar breadth (CONW) plotted against mandibular ramus height (CONHT). ◆ Gorilla; ■ Pongo; ▲ Pan; × Homo.

accounts for 62 % of the total variance, there is a cline between *Homo sapiens*, *Pan*, *Pongo* and *Gorilla*, but all the distributions of the 4 species overlap with the exception of *Pan* and *Gorilla*. *Pan* lies within the middle three fifths of the range covered by *Homo sapiens*. The measurements with the highest variable
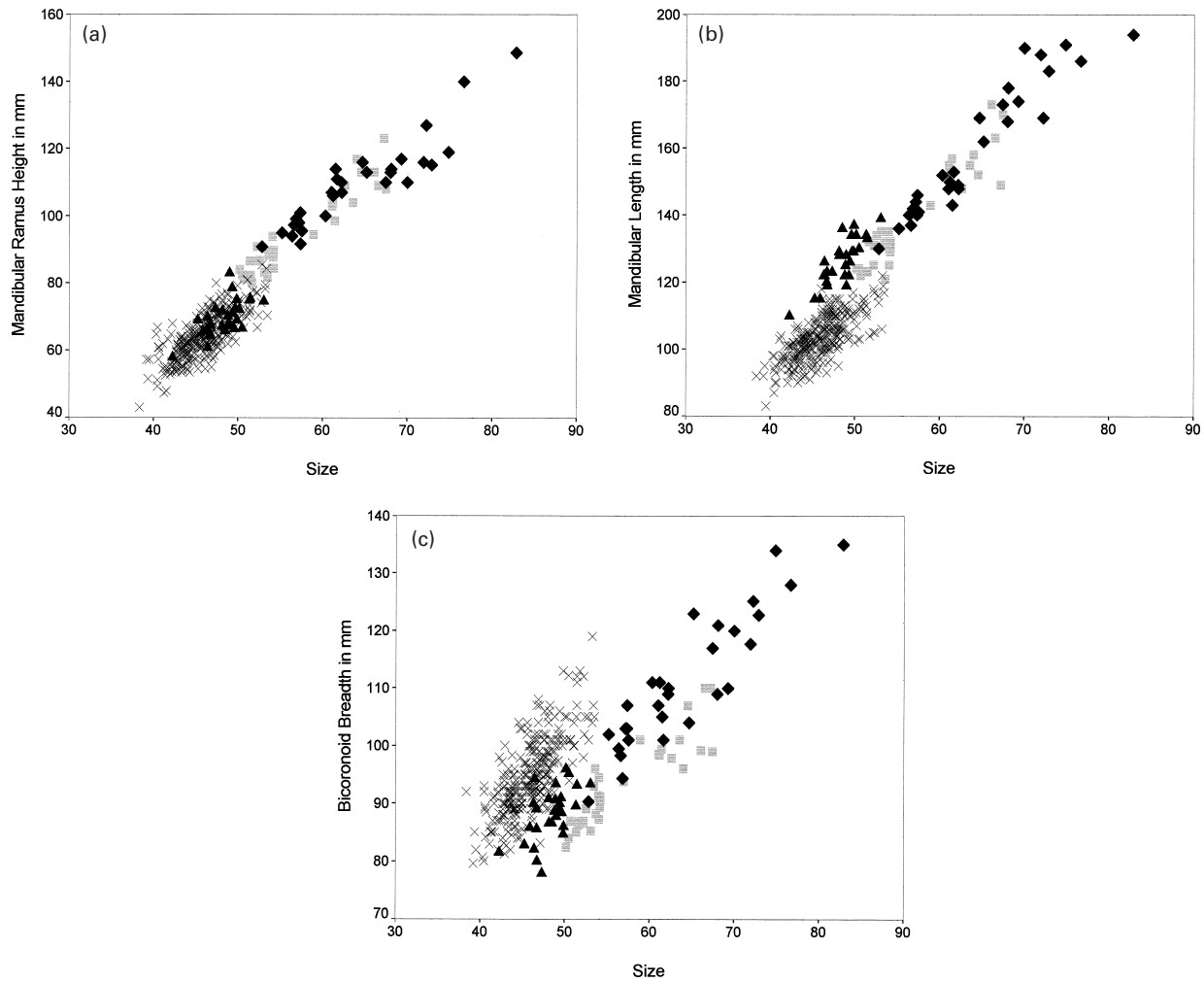
Fig. 4. Bivariate plots of mandibular dimensions in the 4 species scaled against mean mandibular size: (*a*) mandibular ramus height (CONHT); (*b*) mandibular length (MANDL): (*c*) bicoronoid breadth (BICOR). ◆ Gorilla; ■ Pongo; ▲ Pan; × Homo.
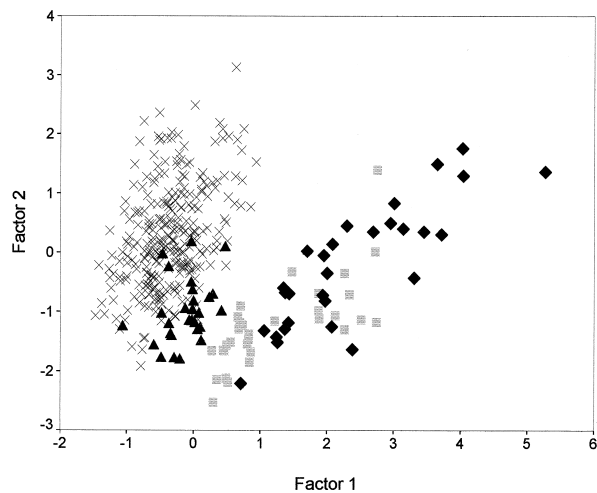
Fig. 5. Plot of factor 2 against factor 1 from a principal components analysis of mandibular dimensions in 4 hominoid species. ◆ Gorilla; ■ Pongo; ▲ Pan; × Homo.

loadings on factor 1 fully or partially reflect the size of the mandibular ramus (CONHT, CONW, NTHT, MANDL, RAMAP). On factor 2, which accounts for

12.6% of the total variance, there is extensive overlap between all 4 species, although *Pan* falls entirely within the lower half of the range covered by *Homo sapiens*. The measurements which reflect the breadths of the mandible (BIM1, BILING, BICOR) have the highest variable loadings on factor 2. The combination of factors 1 and 2 (Fig. 5) separates *Pan* and *Homo sapiens* from *Pongo* and *Gorilla*. Discriminant analysis was used to determine how accurately the 4 species samples could be classified on the basis of the 13 mandibular dimensions. All specimens used in this study were correctly classified by 3 discriminant functions.

Sexual dimorphism

Mandibular sexual dimorphism was compared in *Pan*, *Gorilla*, *Pongo* and modern human samples from Europe (Spitalfields) and South Africa (Zulu). Mean values and standard deviations of each of the variables for males and females from these 5 samples are shown

in Table 3. Differences in male and female variances were tested using Levene's test. Males and females had significantly different variances in 6/13 variables in *Pongo*, 3/13 variables in *Gorilla*, 2/13 variables in the Zulu and Spitalfields samples but in none of the variables in *Pan*. Differences in male and female means were tested for significance using Student's *t* test, using an assumption of equal or unequal variance as appropriate. Males are significantly larger than females in all of the variables in *Pongo*, *Gorilla* and the Spitalfields sample and 8/13 variables in the Zulu sample. In this sample of *Pan troglodytes troglodytes*, the only variable exhibiting a significant difference in male and female size is the thickness of the mandibular body in which females are larger.

Sexual dimorphism in each variable is calculated as (mean male size / mean female size) × 100. Throughout this paper, the magnitude of sexual dimorphism describes the extent to which males are bigger than females. The magnitude of sexual dimorphism among the variables in each of the 5 samples is shown in Figure 6. *Gorilla* exhibits the highest sexual dimorphism in 9/13 variables and *Pongo* exhibits the highest sexual dimorphism in the remaining 4 variables. The *Pan* sample exhibits the lowest sexual dimorphism in all the variables, and females are larger than males in 8/13 variables. The Spitalfields sample exhibits higher sexual dimorphism than the Zulu sample in all of the variables apart from the heights of the mandibular notch and ramus.

Nonparametric rank-order correlations (Sokal & Braumann, 1980) were used to examine whether the 5 groups differ from one another in the distribution of variables showing relatively high or low sexual dimorphism (i.e. the pattern of sexual dimorphism). This method has previously been used to examine similarity in the patterning of coefficient of variation profiles among humans and the African apes (Kramer et al. 1995). Two groups are considered to have similar patterns of sexual dimorphism if, when the variables are ranked by the magnitude of sexual dimorphism, the rank order of the 2 groups are similar and the rank order correlation is significant. Kendall's Tau rank order test examines the null hypothesis that a pair of profiles are uncorrelated. A significant *P* value ($P < 0.05$) therefore demonstrates significant similarity in the sexual dimorphism profiles of the 2 groups being compared, indicating a similar pattern of sexual dimorphism. A nonsignificant result suggests that the 2 groups have different patterns of sexual dimorphism.

Three separate tests were carried out. For the first test, each variable was allocated a unique rank (i.e. no ties were recognised). In subsequent tests, variables with similar magnitudes of sexual dimorphism were assigned the same rank. As the magnitude of sexual dimorphism is measured on a continuous scale (as mean male size divided by mean female size), decisions about which variables to allocate tied ranks were based on the amount of difference in sexual dimorphism between adjacent variables, in an array of variables ranked by the magnitude of sexual dimorphism. For the second test, a new rank was assigned each time this difference exceeded 1 and variables separated by a difference of less than 1 were considered to exhibit the same rank. For the third test a new rank was assigned each time the difference in the magnitude of sexual dimorphism of successively ranked variables exceeded 2. In all 3 tests, the profiles of *Pongo* and the Spitalfields samples were most closely correlated, followed closely by *Pongo* and *Gorilla* and then *Gorilla* and Spitalfields. The sexual dimorphism profile of *Pan* is not like that of any other sample used in this study. The sexual dimorphism profile of *Pongo* is significantly correlated with those of *Gorilla* and both human groups, indicating a similar pattern of sexual dimorphism. The sexual dimorphism profile of the *Gorilla* sample is significantly correlated with that of the Spitalfields sample but not with the profile of the Zulu sample. With the first test, the sexual dimorphism profiles of the Spitalfields and Zulu samples were not significantly correlated, but in subsequent tests these 2 profiles were significantly correlated suggesting a similar pattern of sexual dimorphism. The results of the second rank order correlation test are presented in Table 4.

Despite some diversity in the pattern of sexual dimorphism exhibited by the 5 samples, some predictions can be made regarding relative levels of sexual dimorphism in different mandibular dimensions. In *Gorilla*, *Pongo*, and both human samples, sexual dimorphism tends to be lowest in measurements of mandibular width (the only exception is the width of the mandibular condyle), and highest in measurements of mandibular height. In *Pan*, the heights of the mandible show both the highest and lowest magnitudes of sexual dimorphism for this sample. In all the samples, sexual dimorphism in variables which reflect the size of the mandibular ramus is on average higher than in variables which measure the size of the mandibular body.

Separate principal components analyses were carried out for each of the 5 groups. In both *Pongo* and *Gorilla*, factor 1 accounts for more than 70% of the variance and none of the remaining factors have an

Table 3. *Sample sizes, means and standard deviations for each of the* 13 *mandibular dimensions in samples of males and females from* 2 *modern human populations and* 3 *great ape species*

		Males			Females		Significance	
	n	Mean	S.D.	n	Mean	S.D.	*t* test	Levenes
Spitalfields								
Notch depth	15	13.3	1.5	15	11.2	1.2	**	ns
Body thickness	15	13.1	1.5	15	11.7	1.1	**	ns
Condyle width	15	20.9	1.7	15	17.9	1.7	**	ns
Coronoid-condyle	15	27.3	3.7	15	24.6	2.5	*	*
Body height	15	29.9	2.4	15	26.9	2.5	**	ns
Mandibular breadth	15	38.2	2.4	15	35.7	2.6	**	ns
Symphysis height	15	33.8	2.9	15	29.5	2.7	**	ns
Ramus width	15	30.7	3.5	15	27.3	2.5	**	ns
Notch height	15	46.0	5.5	15	41.1	3.2	**	*
Bilingual breadth	15	79.8	4.2	15	70.5	3.4	**	ns
Ramus height	15	70.4	4.5	15	62.9	3.3	**	ns
Bicoronoid breadth	15	93.3	4.4	15	87.9	5.0	**	ns
Mandibular length	15	105.3	5.4	15	94.7	4.6	**	ns
Zulu								
Notch depth	14	13.2	1.8	16	11.4	1.5	**	ns
Body thickness	14	13.2	1.2	16	12.6	1.5	ns	ns
Condyle width	14	20.8	1.9	16	18.2	1.8	**	ns
Coronoid-condyle	14	34.9	3.0	16	32.4	3.5	ns	ns
Body height	14	31.7	2.4	16	29.0	4.1	*	*
Mandibular breadth	14	34.6	1.9	16	34.0	1.9	ns	ns
Symphysis height	14	35.1	2.3	16	33.3	3.7	ns	ns
Ramus width	14	35.9	3.7	16	34.5	3.3	ns	ns
Notch height	14	47.0	4.9	16	41.1	5.2	**	ns
Bilingual breadth	14	77.2	3.1	16	71.4	3.5	**	ns
Ramus height	14	66.3	4.1	16	57.2	6.0	**	ns
Bicoronoid breadth	14	94.6	4.2	16	90.6	2.3	**	*
Mandibular length	14	107.7	6.3	16	102.3	5.9	*	ns
Gorilla								
Body thickness	13	19.1	1.5	17	17.3	1.1	**	ns
Condyle width	13	36.9	4.8	17	29.6	2.8	**	ns
Coronoid-condyle	13	39.2	5.8	16	34.1	3.2	**	ns
Body height	13	42.2	4.8	17	35.1	3.2	**	ns
Mandibular breadth	13	33.7	2.0	17	30.8	1.9	**	ns
Symphysis height	13	53.3	6.4	17	41.1	3.7	**	ns
Ramus width	13	70.9	8.0	17	52.8	2.2	**	**
Notch height	13	93.2	10.9	17	77.5	7.3	**	ns
Bilingual breadth	13	94.2	8.7	17	79.5	5.1	**	ns
Ramus height	13	119.9	11.8	17	101.6	7.3	**	ns
Bicoronoid breadth	13	120.5	9.2	17	104.1	6.8	**	ns
Mandibular length	13	178.8	10.4	17	143.6	6.1	**	**
Pan								
Notch depth	14	10.7	1.1	14	11.7	1.6	ns	ns
Body thickness	14	12.9	0.9	14	14.2	1.2	**	ns
Condyle width	14	22.4	1.7	14	22.0	1.4	ns	ns
Coronoid-condyle	14	33.9	3.7	14	34.7	4.8	ns	ns
Body height	14	27.7	2.0	14	29.0	2.9	ns	ns
Mandibular breadth	14	35.0	2.2	14	35.2	2.4	ns	ns
Symphysis height	14	37.8	4.1	14	34.5	3.7	ns	ns
Ramus width	14	44.3	4.8	14	43.7	3.0	ns	ns
Notch height	14	53.8	5.2	14	51.5	3.7	ns	ns
Bilingual breadth	14	71.1	5.1	14	71.9	4.5	ns	ns
Ramus height	14	70.7	6.2	14	68.4	4.0	ns	ns
Bicoronoid breadth	14	86.8	4.4	14	89.6	4.6	ns	ns
Mandibular length	14	125.6	7.6	14	126.5	7.0	ns	ns
Pongo								
Notch depth	14	15.8	2.6	19	11.8	1.5	**	ns
Body thickness	14	17.0	2.0	19	14.7	1.0	**	ns
Coronoid-condyle	13	43.9	5.6	19	38.5	3.1	**	*
Body height	14	41.8	5.4	19	35.0	2.5	**	ns

Table 3 (*cont.*)

		Males			Females		Significance	
	n	Mean	S.D.	n	Mean	S.D.	*t* test	Levenes
Mandibular breadth	14	35.8	4.0	19	33.4	1.7	*	**
Symphysis height	14	50.7	6.8	19	42.1	4.0	**	ns
Ramus width	14	57.4	7.2	19	46.0	2.9	**	**
Notch height	14	81.8	9.7	19	67.0	4.7	**	ns
Bilingual breadth	14	82.5	6.7	19	72.9	3.6	**	*
Ramus height	14	107.1	10.9	19	86.8	4.9	**	*
Bicoronoid breadth	14	100.1	6.8	19	89.4	3.9	**	ns
Mandibular length	14	154.9	11.4	19	129.3	6.2	**	ns

ns, nonsignificant; * significant ($P < 0.05$); ** highly significant ($P < 0.01$).
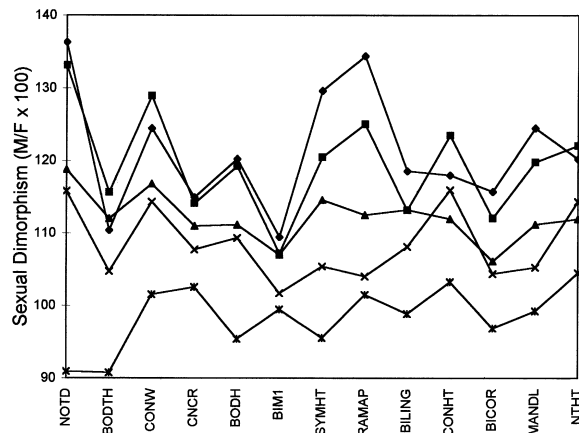
Fig. 6. Plots comparing the amount and pattern of sexual dimorphism in the 13 mandibular dimensions in 5 samples. ◆ Gorilla; ■ Pongo; ▲ Pan; × Spitalfields; ∗ Zulu.

sample, factor 1 accounts for 52.8 % of variance and is the best single discriminator between males and females, but a better separation is obtained using a combination of factors 1 and 2. Similarly, in the Zulu sample, factor 1 is the single best discriminating variable between males and females, but a better separation is obtained by combining factors 1 and 3. In *Pan*, males and females show extensive overlap on each of 5 factors. The variables with the highest loadings on factor 1 differ between the 5 groups, but in all cases, mandibular length occurs among the 5 variables with the highest factor loadings, and in all the groups except *Pan*, mandibular ramus height has the first or second highest loading.

eigenvalue greater than 1. In *Gorilla*, males and females are entirely separated by factor 1. In *Pongo*, all the males and females have separate distributions on factor 1 with the exception 2 young adult males which have values that fall within the range of female values. This suggests that mandibular growth in *Pongo* continues beyond the age of dental maturity and that additional criteria should wherever possible be used to define adult specimens. In the Spitalfields

Regional variation within Homo sapiens

Analysis of the variability in the shape and size of the mandible in a geographically representative sample of 10 modern human populations can be used to explore whether there is any regional patterning underlying the morphological diversity of modern human mandibles. The basic statistical parameters for the 10 populations (Table 1) indicate high intraspecific diversity with no obvious regional patterning. The

Table 4. *Kendall's Tau rank-order coefficients and significance for sexual dimorphism profiles*

	Pongo	Gorilla	Spitalfields	Zulu
Gorilla	0.658 (**)	—	—	—
Spitalfields	0.705 (**)	0.635 (**)	—	—
Zulu	0.541 (*)	0.290 (ns)	0.496 (*)	—
Pan	0.041 (ns)	−0.056 (ns)	−0.136 (ns)	0.206 (*)

ns, nonsignificant; * significant ($P < 0.05$); ** highly significant ($P < 0.01$).
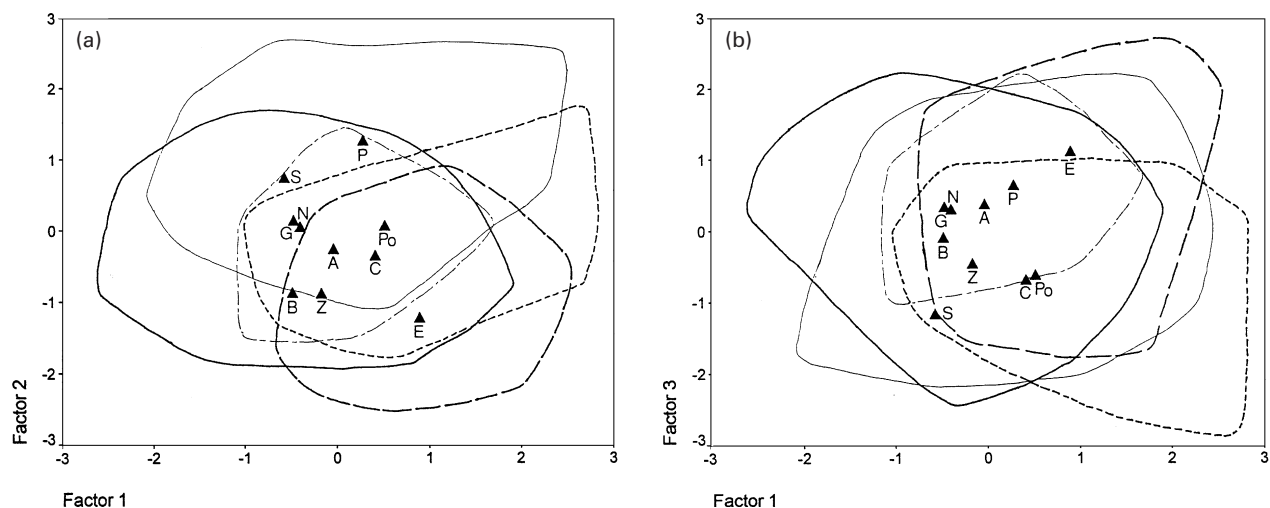
Fig. 7. Plots from a principal components analysis of mandibular dimensions of 10 modern human populations illustrating the 10 population means and the distribution of individuals from 5 geographical regions: (*a*) plot of factor 2 against factor 1; (*b*) plot of factor 3 against factor 2. A, Australian; B, Bushman; C, Chinese; E, Eskimo; G, Gabon; N, Nubian; Po, Polynesian; P, Poundbury; S, Spitalfields; Z, Zulu. —— (heavy), Africa; – – – –, Asia/Arctic; – · – · –, Australia; —— (light), Europe; - - - - -, Polynesia.

greatest variability, as indicated by the coefficient of variation of the 10 population means, occurs in the measurements of the mandibular ramus, particularly the distance between the coronoid process and mandibular condyle, and mandibular ramus width. The Australians have a shallow mandibular notch but for all of the other variables they have values which are close to the mean size of the 10 populations used in this study. The 4 African populations have relatively small mandibles with low mandibular condyle heights and posteriorly narrow mandibles (BILING, BICOR). The 2 European groups have narrow mandibular rami. The Asian/Arctic groups have the largest mandibles, with thick and high mandibular bodies, high mandibular symphyses and a large distance between the coronoid process and mandibular condyle, but are clearly differentiated by the width of the mandibular ramus.

Principal components analysis was used to determine whether there are any regional patterns in the distribution of mandibular shape and size. The distribution covered by individuals from 5 regional groups is illustrated in Figure 7*a* (factor 2 plotted against factor 1) and 7*b* (factor 3 plotted against factor 1). There is a high degree of overlap between the distribution clouds of the 5 regional groups suggesting weak regional patterning. Australia is centrally distributed, and falls almost entirely within the distribution of the African group on all 3 factors. The Asian/Arctic groups and Polynesians show higher values on factor 1 than the other groups. The variables with the highest loadings on factor 1, which accounts for 40.9 % of the total variance, are bilingual distance, mandibular condyle height and mandibular

body height. The European group shows higher values on factor 2 than any of the other groups and the Asian/Arctic group has the lowest values. The variables with the highest loadings on factor 2, which accounts for 14 % of the total variance, are mandibular breadth at the first molar (BIM1), together with mandibular ramus breadth (RAMAP) and the distance between the coronoid process and mandibular condyle (CNCR), which are negatively correlated with factor 2. There is no apparent patterning in the distribution of populations on factor 3, which accounts for 9.7 % of the total variance.

The 10 population means have been superimposed onto Figure 7*a* and 7*b* and the individual population distributions were also examined. The samples from Nubia and Gabon have almost identical values for the population means on all 3 factors and very similar clouds of individual data points. The Bushman and Zulu samples have similar values on factors 2 and 3. The Chinese sample emerges as more similar to the Polynesian sample than to the Eskimo sample on all 3 factors. Spitalfields and Poundbury have similar values on factor 2, reflecting the fact that both European groups have narrow mandibular rami, but are widely separated on factors 1 and 3.

Discriminant analysis was used to determine how accurately population affiliation could be predicted on the basis of mandibular morphology. The first analysis investigated the percentage of mandibles which were correctly assigned to the 5 geographical regions (Table 5). Overall, 78.4 % of mandibles were assigned to the correct geographical region, with the highest proportion of African mandibles correctly classified (85.5 %) and the lowest proportion of Australians

Table 5. *Sample size and percentage of mandibles from 5 regional groups assigned to different regions on the basis of discriminant functions*

		Predicted group membership (in %)				
Region	Number	Africa	Europe	Polynesia	Asia/Arctic	Australia
Africa	110	**85.5**	5.5	2.7	2.7	3.6
Europe	71	11.3	**83.1**	4.2	0.0	1.4
Polynesia	33	15.2	6.1	**78.8**	0.0	0.0
Asia/Arctic	43	25.6	2.3	0.0	**69.8**	2.3
Australia	25	28.0	8.0	0.0	16.0	**48.0**

Table 6. *Sample size and percentage of mandibles correctly assigned to one of* 10 *populations on the basis of discriminant functions. The percentage of misclassified mandibles incorrectly placed in each regional group is also shown*

			Region if incorrectly classified (in %)				
Population	Number	Correct (%)	Africa	Europe	Polynesia	Asia/Arctic	Australia
Eskimo	26	96.2	—	—	—	—	3.8
Poundbury	41	92.7	2.4	2.4	—	—	2.4
Spitalfields	30	90.0	3.3	—	6.7	—	—
Polynesian	33	81.8	12.1	3.0	—	3.0	—
Chinese	17	76.5	—	17.7	—	—	5.9
Nubian	40	65.0	20.0	7.5	—	2.5	5.0
Zulu	30	60.0	16.6	—	3.3	16.6	3.3
Australian	25	60.0	28.0	4.0	—	8.0	
Gabon	32	50.0	31.3	9.4	—	—	9.4
Bushman	8	25.0	75.0	—	—	—	—

(48.0%). The second analysis determined the percentage of mandibles from each of the 10 populations which were correctly assigned (Table 6). Overall, 73.4% of mandibles were assigned to the correct population. The least successfully classified mandibles were those from the 4 African populations, many of which were misclassified as belonging to other African groups, and those from Australia. Forty percent of mandibles that were incorrectly classified were placed in a different population in the same geographical region, but it is only among the African populations that misclassified cases could be considered to be anything other than randomly distributed. Among the 4 African groups, 62% of misclassified cases were incorrectly predicted to belong to a different African group, whereas only 39% of the total sample of mandibles are from Africans.

DISCUSSION

In this paper we have documented differences in the mandibular morphology of 3 great apes and in 10 populations of modern humans. While determined either by genetic or environmental influence or both, these differences in the shape and size of adult mandibles must result from differences in growth and remodelling. Similarly, differences in morphology between modern human and other living or extinct hominoids must result from differences in growth rate or duration and the degree and type of remodelling at key locations on the mandible that take place from before birth until adulthood. With this in mind we discuss first interspecific variation in mandibular form and then intraspecific variation, sexual dimorphism and regional variation in the human mandible.

Interspecific variation in mandibular morphology

Comparison of the mandibular morphology of *Homo sapiens*, *Gorilla*, *Pan* and *Pongo* demonstrates that *Homo sapiens* has a short mandible, reflected both in the measurements of mandibular length and in the width of the ramus. It is also clear that *Pan* and *Homo sapiens* have lower mandibular bodies and a lower ramus than *Gorilla* or *Pongo*. When evaluated relative to overall size (calculated here as the geometric mean of the 13 mandibular dimensions), the human mandible is shown to be wide, particularly across the mandibular condyles, and slightly shorter than expected, whereas the chimpanzee mandible is rela-

tively long. The relationships between some pairs of variables, particularly those which measure the height of the mandibular body exhibit a tight linear relationship with each other and against mandibular size. The low absolute values for mandibular condyle height and the height of the mandibular body in *Pan* and *Homo sapiens* are a result of their smaller overall size.

While it is self evident that humans are less prognathic than great apes, it may not have been so obvious that *Pan* has such a relatively long mandible. This may relate to the large anterior dentition in *Pan*, that is huge in proportion to the molars and premolars (Swindler, 1976). It is unlikely that large anterior teeth would be associated with a long mandible simply to gain additional alveolar support, but a long mandible with a low ramus would increase gape anteriorly, and this might have some influence on the ability of chimpanzees to undertake certain types of food preparation such as peeling, paring and stripping of fruit more effectively. Kieser et al. (1996, 1999) have shown, at least for humans, that for a given jaw width, the longer the jaw the lower the maximum bite force on the working side (see also below). The smaller molar size together with the long mandible in *Pan* may also be a reflection that this relationship holds true in great apes. It may follow that any advantage achieved from increased gape anteriorly is likely to be associated with a reduced maximum bite force (and maybe smaller teeth) posteriorly.

The great width of the human mandible between the condyles may also be related to bite force (Kieser et al. 1996, 1999) and shows some independence from the width of the cranium. The articulation of the condyles at the temporomandibular joint varies in its relation to the cranial vault among hominoids, lying beyond (laterally) in great apes and early fossil hominids (including *Homo erectus*), but beneath in modern humans. This suggests independence (or even an inverse relation) between any masticatory adaptations and the expanding neurocranium. However, human crania vary greatly in their breadths, and in the broadest crania the width between the condyles may be influenced by this nonmasticatory factor, since neurovascular structures would be compromised if the condyles constrained them by not widening apart. Obviously, soft tissues, especially muscles, play a key role in shaping mandibular form (Hunt, 1998). For example, large cross sectional areas of the medial pterygoid and temporalis muscles correlate with brachycephaly and with a long mandible (Weijis & Hillen, 1984). The relationship between cranial base morphology and the functional constraints of mandibular width and length on maximal bite force generation is worthy of further study.

Intraspecific variation in Homo sapiens

This study documents marked population differences in the shape and size of the mandible within *Homo sapiens*. The most notable variation occurs in the height and breadth of the mandibular ramus, in the same dimensions for which sexual dimorphism tends to be highest. The results for ramal width are mirrored in a recent study of 7 regional samples by Anderson (1998) who found that Eskimos had the largest and temperate Europeans the smallest ramal breadths, and that an African (Ugandan) sample was unexceptional in its values. The classic comparative studies of Hunter (1771) and Humphry (1866) established that during the growth of the mandible, bone along the anterior border of the ramus of the mandible is resorbed as bone along the posterior border is deposited. Variation in anteroposterior width of the ramus arises from a balance between these processes and through resorption and deposition on the buccal and lingual aspects of the mandibular ramus (Enlow & Harris, 1964; Enlow, 1990). Population differences can reflect an increase or decrease in the rate or duration of any one of these processes.

Some of the differences in mandibular morphology within and between human groups can be singled out as most likely associated with adaptations to demands on the masticatory system. The Chinese group used in this study, for example, is characterised by tall ascending mandibular rami that raise the temporomandibular joint high above the occlusal plane, with thick mandibular bodies, a tall robust symphyseal region and a widely spread condyle and coronoid process. Many of these are features identified by Hylander (1977, 1979, 1988) and Antón (1996) as associated with powerful masticatory forces that involve torsional bending of the body and at the chin during chewing. The coronoid process of the mandible effectively extends upwards and backwards into the tendon of the temporalis muscle and is presumably influenced by it. Retraction of the jaws beneath the cranium, but at the same time more functional emphasis on and forward migration of the anterior temporalis muscle, may underlie an increase in the distance between the condyle and the coronoid process in some populations. All this, combined with a narrowing of the ramus point to some probable functional explanations for the complex of comparative morphological observations in this region of

the mandible. Interestingly the Eskimo, who are otherwise similar to the Chinese in shape and size, have moderate values for the height of the ramus, but exceptionally wide mandibular rami. These differences may be related to the function of the masseter and medial pterygoid muscles but this cannot be assumed to be the case.

Kieser et al. (1996, 1999) have proposed a mathematical model for hypothetical force distribution between opposing jaws and identified a position on the working side dental arcade where force is maximal ('F max' is approximately in the region of the lower 1st permanent molar). Bite force posterior to this point on the working side gradually reduces. Both the maximal bite force and the rate of force reduction distal to this point are governed by 2 principal factors, jaw length and intercondylar distance. This means that for a given jaw length, the narrower the jaw, the higher the force at 'F max'. Alternatively, for a given jaw width, the longer the jaw the lower the force at 'F max' and the more gradual the posterior reduction in bite force distal to 'F max'.

Mandibular morphology however, is far from being the only factor governing masticatory function. All populations of modern humans (and more than likely great apes as well) contain individuals with contrasting facial and mandibular features, such as relatively short or relatively long and narrow faces. Hunt (1998) has clearly demonstrated the relation between occlusal force and mandibulofacial form in groups of humans. Adults characterised by a large posterior face height, a small anterior face height, a low gonial angle and a tendency towards a 'short square face' can generate large bite forces. Conversely, adults with a high gonial angle, an increased anterior face height and tendency towards a 'long face anteriorly' generate significantly lower maximum occlusal forces. Interestingly, these differences in bite force do not exist in children with these contrasting facial morphologies and seem to develop as the long faced children fail to increase their muscle strength during the adolescent period (Proffit & Fields, 1983). Muscle form and structure, therefore, is as important if not more important than mandibular morphology in determining occlusal force generation. Ongoing investigations into the differences in muscle fibre type expression associated with different facial morphologies are beginning to shed light on the mechanisms responsible for this (Hunt, 1998). It is clear that there is considerable interplay between variation in masticatory function, muscle microstructure and mandibular morphology. Variation in each of these span all human populations and there is much to be learned about interrelations between them.

Sexual dimorphism

The analysis of mandibular sexual dimorphism in modern humans and the extant great apes demonstrates variability in both the pattern and magnitude of sexual dimorphism in the 4 species examined. The differential magnitude of mandibular sexual dimorphism in the 2 human groups is notable and demonstrates the existence of marked intraspecific variation. The relatively high level of sexual dimorphism in the Spitalfields mandible sample is surprising given previous work by Molleson & Cox (1993) which found reduced dental and cranial dimorphism compared with earlier British samples but did not report on the mandibles. The difference in the results of these 2 studies reflects variability and possible independence in the magnitude of sexual dimorphism in different dimensions of the dentition and cranial and post cranial skeleton. Variability in the growth patterns through which sexual dimorphism is attained in different parts the human skeleton has previously been demonstrated (Humphrey, 1998). The difference may also indicate that higher levels of mandibular sexual dimorphism exist in other recent or subrecent human groups.

It is also interesting that in *Pan*, where there is considerable sexual dimorphism in canine size, there is so little sexual dimorphism in the mandible. This suggests a degree of independence between dental and skeletal growth mechanisms in this regard. It also has implications for interpreting the fossil hominid record in that apparently highly sexually dimorphic mandibles, of *Australopithecus afarensis* for example, might (in a developmental sense) be associated with canines that are greatly reduced in their degree of sexual dimorphism. Similarly, the fact that a high degree of sexual dimorphism has been described for the canines of *A. anamensis* (Leakey et al. 1998) need not imply that the mandibles of this species were equally dimorphic.

The results of this study suggest that those groups exhibiting the lowest levels of sexual dimorphism in the mandible are most divergent in their patterns of sexual dimorphism. The patterns of sexual dimorphism in *Gorilla*, *Pongo* and in the Spitalfields sample, which show the highest magnitudes of sexual dimorphism, are significantly correlated. The pattern of sexual dimorphism shown by *Pan troglodytes* is dissimilar to that of any other species. It is particularly notable that the 2 human samples, which differ in their magnitude of sexual dimorphism, both resemble *Pongo* in their pattern of sexual dimorphism more closely than one another (although all 3 of these

sexual dimorphism profiles are significantly correlated). This raises the possibility that *Pongo* is the most conservative in its pattern of sexual dimorphism and that the other groups have diverged in different ways from that which may be close to a common ancestral pattern. An alternative possibility is that the *Pan* and Zulu samples used here appear to show a divergent pattern of sexual dimorphism from other samples simply because they lack significant sexual dimorphism in many dimensions. It remains a possibility that comparatively small samples such as those used in this study generate sampling error and future studies on larger numbers of individuals from carefully defined subspecies may or may not confirm the results presented here.

The findings of this study differ from those of an earlier analysis of sexual differences in humans and great apes. Wood et al. (1991) found 2 patterns of mandibular sexual dimorphism, with the first applying to *Gorilla* and *Pongo* and the second version to *Pan* and *Homo sapiens*. In contrast, this study did not reveal any similarities in the pattern of sexual dimorphism between *Homo sapiens* and *Pan*. The sample of *Pan* used here comprises *Pan troglodytes troglodytes* from Cameroon, whereas the Wood et al. (1991) studied *Pan troglodytes verus*. The difference between the findings of the 2 studies may be indicative of intraspecific variation in the pattern of mandibular sexual dimorphism within the common chimpanzee. Shea & Groves (1987) have noted that the 3 subspecies of *Pan troglodytes* exhibit divergent patterns of dimorphism, and that the relative magnitude of sexual dimorphism among different subspecies may vary in different parts of the skeleton. This suggests that more extensive studies of the pattern of intraspecific variation in mandibular sexual dimorphism should be undertaken in order to fully explore the effects of subspecific and geographical differences. While not to do with mandibles, it is interesting to note that O'Higgins et al. (1990) reported differences in the pattern of sexual dimorphism between samples of modern British and Chinese crania and it may simply be that intraspecific sexual dimorphisms are much more variable than has hitherto been appreciated.

Wood (1985) suggested that measures of sexual dimorphism could be used in phylogenetic analyses. Several different aspects of sexual dimorphism could be examined for their potential usefulness as phylogenetic indicators, including the magnitude and pattern of sexual dimorphism within a species and the ontogenetic pathways which give rise to these differences. Since this study is based on mature specimens it has only been possible to examine the magnitude and pattern of sexual dimorphism in adults. Within this sample of only 4 species it would be difficult to determine with any certainty whether variation in the magnitude and pattern of sexual dimorphism among different species has any phylogenetic significance. However, it is clear that among the extant large bodied hominoids there is a poor overall correspondence between the pattern of sexual dimorphism in mandibular dimensions and the phylogenetic relationships of the species concerned. The results of this study indicate that both the magnitude and pattern of sexual dimorphism can change rapidly and are therefore poor indicators of phylogenetic relationships. Mandibular size and sexual dimorphism are reduced in *Pan* and *Homo sapiens*, and while it would be tempting to interpret this reduction as a shared derived character of the 2 species, there is no supporting evidence. Comparative analysis of the mandibular growth patterns of humans, gorillas and chimpanzees demonstrates that the differences between chimpanzees and gorillas can be largely accounted for by differences in growth rate, whereas the human growth trajectories differ markedly (Humphrey, 1999). Furthermore, the presence of mandibles that are highly variable in size in the hominid fossil record cautions against this interpretation.

That different mandibular measurements differ in their magnitude of dimorphism in *Pan* and *Homo sapiens* as well as intraspecifically between different human populations implies that patterns of sexual dimorphism are not under tight genetic control or conserved over long periods of time. Almost any site of mandibular bone deposition, or resorption, or remodelling for that matter, seems to have a potential for becoming sexually dimorphic. It is clear nonetheless, that the sites associated with the greatest morphological changes in size and remodelling during growth, those that involve the mandibular condyle and ramus in particular, are generally the most sexually dimorphic in the species examined here. In this respect the findings of this study support previous analyses of mandibular sexual dimorphism (Martin, 1936; Morant et al. 1936; De Villiers 1968 *a, b*; Hunter & Garn 1972). These results partially support the observation by Aitchison (1963*b*) that there are consistent sexual differences in the mandibular notch. The depth of the mandibular notch proved to be highly dimorphic in all of the samples except *Pan* but the distance between the coronoid process and mandibular condyle was not particularly sexually dimorphic.

It is tempting to infer that differences in rates and in

the periods of growth at the mandibular condyle are primarily responsible for differences in mandibular length. However, resorption of bone at the symphysis in *Homo sapiens* may play a key role in reduction of jaw length (Enlow & Harris, 1964). It is also clear that a greater rate of resorption at the anterior border of the ramus of the mandible in *Homo sapiens* would contribute to a reduction in the width of the ramus relative to that in the great apes. Adult dimensions are the result of a balance between resorptive and depository activities at periosteal and endosteal surfaces. It is just as likely that the low mandibular ramus in *Pan* and *Homo sapiens*, for example, results from a reduction in the rate of bone deposition at the angle and lower border of the mandible or at the alveolar crest as from a reduction in the rate of bone deposition at the condyle. The condyle itself will be bigger and wider in individuals where there is least remodelling of bone to narrow the neck, as bone continues to be deposited at the head (Moore & Lavelle, 1974). In short, larger dimensions in the mandible, either between taxa or between males and females, can result from increased deposition of bone, increased resorption of bone, or indeed a reduction in remodelling activity altogether. These observations are testimony to the many complex mechanisms that might underlie sexual dimorphism at different sites in the mandible. It would be incorrect to presume that sexually dimorphic variables always result from more bone deposition in male mandibles. This study highlights the potential for testing this hypothesis in a comparative context at several key anatomical locations on the mandible and might in turn contribute to a better understanding of sexual dimorphism in a phylogenetic sense.

Regional variation in Homo sapiens

Previous work on variation in mandibular morphology suggests that the mandible is less useful for describing population differences than the cranium (Cleaver 1937; Hrdlička, 1940 *b,c*). This study demonstrates that 74.3 % of mandibles can be correctly classified into one of 10 populations using discriminant functions based on a series of 13 measured variables. The results of this mandibular analysis can be compared with a similar study by Howells (1973), who used discriminant functions to predict the population affiliation of crania from 17 human populations, based on a series of 70 measured variables. The first 10 discriminant functions classified 93.2 % of males and 91.9 % of females correctly, with the majority of misclassified crania predicted to belong

to populations from broadly the same geographical region. Comparison of the results of Howell's cranial analysis and the present mandibular analysis suggests that better overall classification at the population level can be achieved using cranial dimensions than using mandibular dimensions. However, the efficacy of cranial data in discrimination may be partly due to the greater number of variables available. Wright (1992), using a subset of 33 of Howells' measurements from his database, found that he could achieve a discriminant function success rate of about 74 % in test classifications, about the same as we have achieved from 13 mandibular measurements.

With the exception of Africa, the geographical regions are too poorly sampled to determine whether there is any evidence of regional patterning in mandibular morphology among the populations used in this study. The sample of mandibles from the African groups were among those least well classified at the population level, but a disproportionate number of the mandibles which were incorrectly classified were wrongly attributed to other African populations. This indicates that there is an African mandibular morphology that is able to accommodate the 4 geographically diverse African groups used in this study, to the partial exclusion of nonAfrican groups.

Some comment is warranted with respect to differences in mandibular morphology that exist between European mandibles from Poundbury and Spitalfields, separated by approximately 1500 years, and which in some respects are as distinct as mandibles of modern Zulus and Eskimos. This observation underscores the potential plasticity of the mandible and demonstrates that some of Hrdlička's (1940 *b,c*) caution about the evolutionary and phylogenetic value of the mandible was warranted. It is perhaps inevitable that the mandible will be less useful than the cranium for identifying the relationships between human populations given this plasticity. Since no equivalent study was carried out on crania of the same individuals included here, and the number of measurements made and individuals included in other studies of crania vary so greatly it is premature to conclude firmly that mandibles are less useful than crania for discriminating between populations. It does nonetheless appear to be the case given the available evidence.

Conclusions

In this study human mandibles were most clearly distinguished from those of great apes by a shorter mandible, a narrow and low ramus, and by a wider distance across the floor of the mouth. Of the great

apes, *Pan* was most similar to *Homo sapiens*, with both species sharing lower values for the height of the mandibular corpus, symphysis and ramus. While *Pongo* and *Gorilla* were the most sexually dimorphic and *Pan* and *Homo sapiens* least dimorphic, there was no common pattern, or distribution, of sexually dimorphic measurements, either within the modern human groups or among apes. It is possible that *Pongo* shows the most conservative, and arguably plesiomorphous, pattern of sexual dimorphism but this is conjectural. Consideration of how growth of the mandible occurs at the sites of the variables measured in this study suggest that larger values for sexually dimorphic variables in males might result from either greater rates of bone deposition, reduced rates of resorption, or even an overall reduction in bone remodelling activity at some sites. The potential growth mechanisms are therefore numerous and may partly explain the variable pattern of sexual dimorphism in different populations of hominoids. Modern human mandibles appear to show less regional variation than do crania, as judged from other studies, although the number of variables available for analysis may be a factor here. Conclusions based on principal components analysis suggest the 4 African populations appear to have a common morphology but that Australian mandibles are closest to the average of all human populations in their shape and size. Multivariate craniometric studies (e.g. Howells, 1973, 1989; Hanihara, 1996) show a basic similarity between African and Australian crania, compared with other regions. Our principal component analysis results are consistent with this finding, in that the Australian samples tended to be nested within the variation of the African groups. Some populations (Chinese in particular) seem to have a morphological complex that fits with possible masticatory adaptations to a tough diet (tall ramus, thick mandibular body, tall robust chin and widely spaced condyle and coronoid process). Surprising differences between subrecent and modern European mandibles imply a considerable degree of plasticity in mandibular morphology through time and underscore the importance of compiling a large database with which to compare fossil hominid mandibles.

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